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Taxonomy of the *Mirafra assamica* complex

PER ALSTRÖM

Four taxa are recognised in the *Mirafra assamica* complex: *assamica* Horsfield, *affinis* Blyth, *microptera* Hume, and *marionae* Baker; *subsessor* Deignan is considered to be a junior synonym of *marionae*. These four taxa differ in morphology and especially in vocalizations. Both *assamica* and *microptera* have diagnostic song-flights, while *affinis* and *marionae* have similar song-flights. There are also differences in other behavioural aspects and habitat between *assamica* and the others. On account of this, it is suggested that *Mirafra assamica sensu lato* be split into four species: *M. assamica*, *M. affinis*, *M. microptera* and *M. marionae*. English names proposed are: Bengal Bushlark, Jerdon's Bushlark, Burmese Bushlark and Indochinese Bushlark, respectively.

The Rufous-winged Bushlark *Mirafra assamica* Horsfield is usually divided into five subspecies: *assamica* Horsfield (1840), *affinis* Blyth (1845), *microptera* Hume (1873), *subsessor* Deignan (1941), and *marionae* Baker (1915) (Peters 1960, Howard and Moore 1991). One further taxon, *ceylonensis* Whistler (1936), is sometimes recognized, but following Ripley (1946) and Vaurie (1951) most recent authors treat it as a junior synonym of *affinis*. The name *marionae* is actually predated by *erythrocephala* Salvadori and Giglioli (1885), but this does not appear to have been used since it was introduced, and I therefore propose that the name *marionae* be conserved.No morphological study of all taxa has been published, but Ali and Ripley (1973) and Vaurie (1951) have made comparisons between *assamica* and *affinis*. The vocalizations, as well as song-flights and other behavioural aspects, are superficially, sometimes even incorrectly, described in the literature (*assamica* and *affinis*, Ali and Ripley 1973; *microptera*, Smythies 1986 [incorrectly referred to therein as *assamica*]; and *marionae*, Boonsong and Round 1991). This study compares all five taxa with respect to morphology, and the ones which I consider valid are thereafter compared with respect to vocalizations, behaviour and habitat choice, on which bases I propose that they are better treated as four separate species.

Mirafra assamica sensu lato breeds from the Indian subcontinent to Vietnam (Fig. 1). *M. a. assamica* occurs in northern India south to northern Madhya Pradesh and northernmost Orissa, east through Nepal, Bangladesh, and westernmost Myanmar (Burma). *M. a. affinis* occurs in southern India north to southeasternmost Bihar and southernmost West Bengal (Ball 1874, 1878), and in Sri Lanka. *M. a. microptera* is endemic to central Myanmar. *M. a. subsessor* is found in northern Thailand, and *marionae* in southern Burma (Tenasserim), Thailand except north and peninsula, Cambodia, and southern Vietnam. (Peters 1960, Howard and Moore 1991).

MATERIAL AND METHODS

I studied each of these taxa in the American Museum of Natural History, New York, USA and the Natural History Museum, Tring, U.K. (100+ *assamica*, *c.* 90 *affinis*, *c.* 45 *microptera*, 30+ *marionae*, and 2 *subsessor*). Pamela C. Rasmussen examined 6 further specimens of *subsessor* (including the holotype) on my behalf in the Smithsonian Institution, Washington, D.C., USA. I have examined *c.* 20 specimens of *ceylonensis*, though I have not compared it in detail with *affinis*, and I have only measured four specimens (of which two were unsexed). For all taxa, measurements of wing length (with the wing flattened and stretched; method 3, Svensson 1992), tail length, bill length (to skull), bill depth (at distal end of nostrils), tarsus length and hind-claw length were taken of specimens whose labels indicated their sex.

I studied *assamica* in the field in northern India (Haryana, Uttar Pradesh, West Bengal and Assam) and Nepal during several visits in the period 1983-1997; *affinis* in central and southern India (Andhra Pradesh, Kerala and Tamil Nadu) in February 1993; *microptera* in Myanmar in late March/early April 1996; and *marionae* in Thailand in April 1991, March 1992 and April 1996. At least 50-100 individuals of each taxon were observed, and a large proportion of these were heard singing/calling and seen in song-flight. I have not observed *subsessor* in the field.

I tape-recorded songs and calls of *assamica*, *affinis*, *microptera* and *marionae* (*c.* 10 individuals of each taxon), using a Sony WM-D6 cassette recorder, a Sony TCD-D3 DAT recorder or a Sony TCD-D7 DAT recorder and a Telinga Pro parabolic reflector/microphone (mono). I also obtained tape-recordings made by others: three individuals of *affinis* from Karnataka and Tamil Nadu (Claude Chappuis), three *affinis* from Tamil Nadu (Paul Holt), two *affinis* from Tamil Nadu (Sivaprasad 1994; wherein scientific name is wrongly given as *Mirafra erythroptera*, Indian Bushlark), and one *microptera* from central Myanmar (Craig Robson).

I produced sonagrams of most of the individuals I tape-recorded, using the computer software SoundEdit Pro/ SoundEdit 16 (version 2) from Macromedia and the software Canary 1.2 (Mitchell *et al.* 1995). The sound analysis terminology used in this paper is explained in Fig. 2. The term 'note' refers to any discrete sound unit.

In Myanmar, I searched for sympatry between *microptera* and *assamica* and *microptera* and *marionae*. I made many stops in different habitats along the road between Prome (Pyè)-Taungdwingyi-Magwe-Pagan (Bagan)-Myingyan-Mandalay-Meiktila-Pyinmana and from Pegu-Yangon (names from *The Times Atlas of the World*, comprehensive edition, 1993; route shown in more detail in Nelles Maps, Burma [no year given]). In the Myingyan district in central

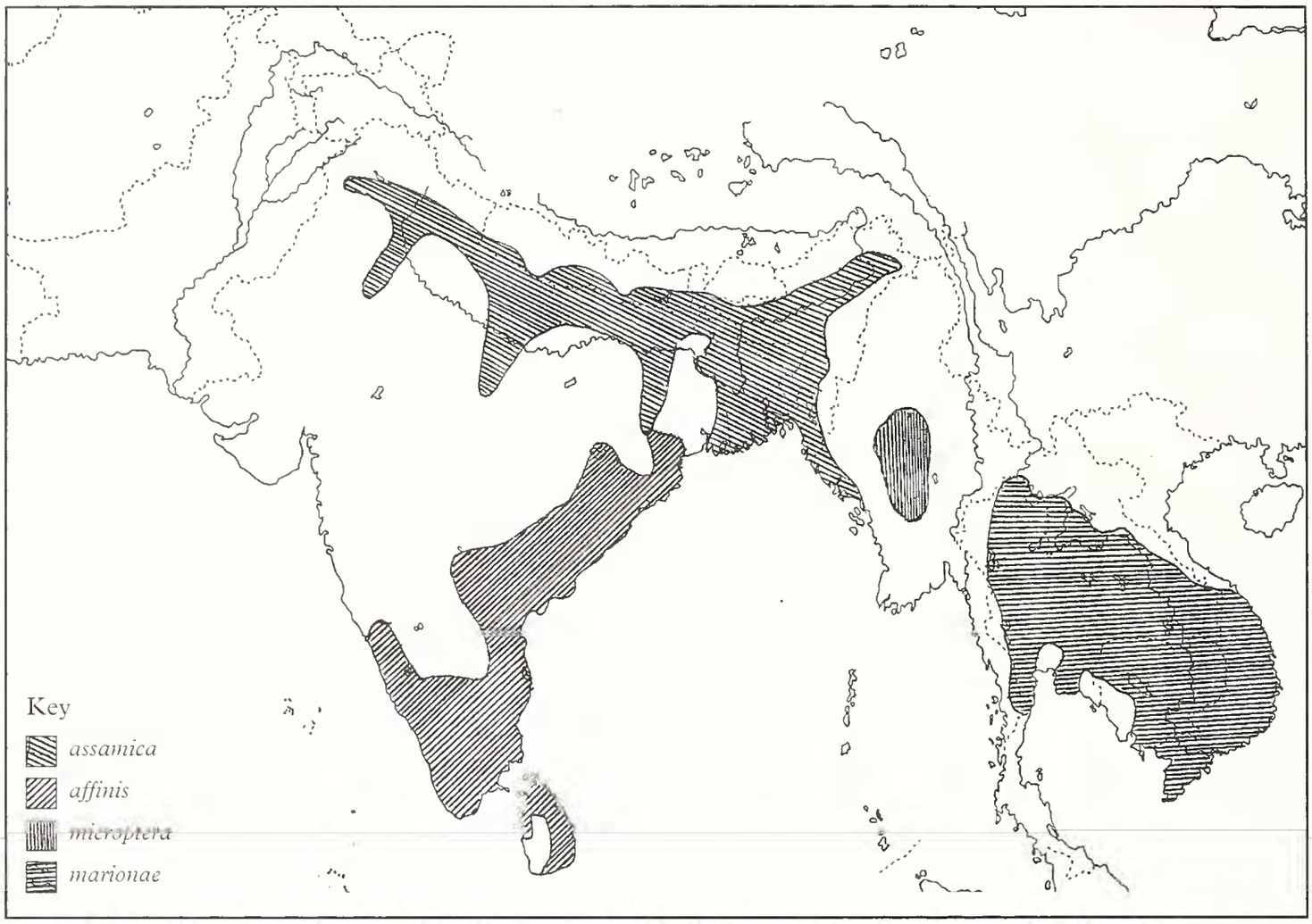

Figure 1. Map showing distributions of the four taxa in the *Mirafra assamica* complex. Drawing: Per Alström

Myanmar, where both *assamica* and *microptera* have been said to occur (Macdonald 1906), I checked most places with habitats which appeared to be suitable for *assamica*.

RESULTS

Morphology

According to Deignan (1941) *subsessor* differs from *marionae* in having 'the prevailing tone of the upperparts gray, as in *assamica*, not rufescent, as in *marionae*'. I was, however, unable to find any differences between *subsessor* and *marionae*, and Pamela C. Rasmussen (*in litt.*) comments that it is just barely perceptible that *marionae* is a bit more rufescent above than *subsessor*, and that 'whether subspecific denomination is merited is arguable'. The measurements do not support that *subsessor* be upheld as a separate taxon (Table 2). Accordingly, *subsessor* is here treated as a junior synonym of *marionae*. The taxon *ceylonensis* was originally described on the basis of being slightly longer-billed and slightly darker (Whistler 1936; see also Whistler 1944). I have not compared *ceylonensis* and *affinis* in detail, but Vaurie (1951) concluded that *ceylonensis* ought to be treated as a junior synonym of *affinis*. However, Abdulali (1976) stated 'I have already referred (in press) to the validity of this large-billed race, with and without rufous underparts, occurring in Ceylon and in a very restricted area in southernmost India.' No relevant publication has been traced and *ceylonensis* is regarded as invalid pending further information.

The plumage differences between *assamica*, *affinis*, *microptera* and *marionae* are slight and overlap to a great degree, and I cannot find any single character to be diagnostic. However, by using a combination of characters (Table 1), each taxon can be identified by plumage alone. *M. a. assamica* stands out from the others, in particular because of its less contrasting head pattern and darker underparts. Most of the measurements overlap extensively between the taxa (cf. Table 2). However, the bill is consistently deeper in both sexes of *assamica* than in any other taxon (no overlap in bill depth and bill depth/bill length ratio), and the tail is proportionately longer in males of *microptera* than in the others (little or no overlap in tail/wing ratio) (cf. Table 2). Note that because of sexual dimorphism, the sexes should be compared separately.

Vocalizations

Songs

The song of *assamica* consists of a thin, high-pitched, slightly hoarse, squeaky, usually disyllabic note, which is repeated monotonously at short (*c.* 0.35-0.60 s, sometimes longer) intervals for periods up to a few minutes. It can be transcribed as e.g. *ü(-)eez*, with equal stress on both syllables (Fig. 3a); *ü(-)eez*, with the stress on the second syllable (Fig. 3b); *üü(-)eez*, with the stress on the first syllable; or with an additional note, *üü(-)eez dzreee*. Short spells of what appears to be mimicry of the song of Paddyfield Pipit *Anthus rufulus* are sometimes included, especially during the descent. This song is usually delivered in a song-flight (see Behaviour, below), and only rarely from the ground. It also has a different type of song, which is a slow paced jingle of thin, high-pitched notes and mimicry (Fig. 4). This second type of song is mainly given from the

Table 1. Plumage characteristics (fresh plumages) of the four valid taxa in the *Mirafra assamica* complex. (T means tail feather numbered descendently)

	assamica	*affinis*	*microptera*	*marionae*
Crown	Brownish-grey or grey-brown, relatively indistinctly streaked.	Brownish-buff or rufescent grey-brown, with prominent blackish-brown streaks.	Brownish-buff or rufescent grey-brown, with prominent blackish-brown streaks.	(Rufescent) grey-brown, with prominent blackish-brown streaks.
Nape	Brown-grey or grey-brown, faintly streaked.	Brownish-buff or rufescent grey-brown, with distinct blackish-brown streaks.	Brownish-buff or grey-brown, with distinct blackish-brown streaks.	Grey-brown, with distinct blackish-brown streaks. Usually shows a thin whitish band across upper nape.
Supercilium	Relatively indistinct, buffish.	Relatively narrow, usually more buffish in front of eye than above/behind.	Relatively broad, usually uniformly buffish.	Relatively broad, usually uniformly pale buffish or whitish.
Ear-coverts	Base colour pale brownish; relatively poorly patterned.	Base colour pale grey-brown with dark streaks at rear (generally forming dark rear border).	Base colour pale buffish-brown; distinct dark eye-stripe and rear border, indistinct dark streaking.	Base colour pale brownish with dark streaks at rear (generally forming dark rear border).
Side of nape/ rear ear-coverts	Distinct pale band lacking.	Usually shows rather distinct pale band.	Shows distinct pale band.	Usually shows rather distinct pale band.
Mantle and scapulars	Brown-grey or grey-brown, relatively indistinctly streaked, especially anteriorly	Rufescent grey-brown (usually at least slightly less rufous-tinge than crown), with prominent dark grey-brown or blackish-brown streaks.	(Rufescent) grey-brown, usually contrasting with more warmly coloured crown, supercilium and ear-coverts; prominent dark grey-brown or blackish-brown streaks.	Grey-brown with moderately prominent dark streaks; anterior part of mantle more distinctly streaked than posterior part.
Underparts	Base colour deep rufous-buff. Breast spots dark grey-brown or blackish-brown, slightly diffuse and sometimes relatively small.	Breast buffish when fresh, contrasting slightly with paler buffish belly. Breast-spots large, rounded or more triangular, blackish-brown.	Rather uniformly very pale buffish, generally appearing whitish in the field. Breast-spots large, rounded blackish-brown or blackish.	Base colour buffish with a greyish tinge. Breast-spots generally more diffuse, less rounded, less black and more densely spaced than in *affinis* and *microptera*.
Secondary-coverts, tertials	Dark grey-brown or blackish-brown with pale brownish-buff or rufous-buff tips/edges.	Dark or medium grey-brown with buffish (secondary-coverts) or pale buffish or buffish-white (tertials) tips/ edges.	Dark or medium grey-brown with buffish (secondary-coverts) or pale buffish or buffish-white (tertials) tips/ edges.	Dark grey-brown with pale brownish-buff or rufous-buff tips/ edges.
Rectrices	Dark grey-brown, with diffuse rufous-buff outer edges; on T6	Dark grey-brown, T2-T6 with progressively broader buffy outer edges (T6 with entire or most of outer web). Especially T6 often shows narrow buffish tip to inner web.	T1-T2 dark grey-brown, T3-T6 blackish-brown, T2-T5 with narrow pale outer edges. T6 shows pale buffish or buffish-white	Dark grey-brown, with indistinct rufous-tinged outer edges, widest on T6 (where often reaching shaft);

Table 2. Measurements of *assamica, affinis, microptera* and *marionae* with mean, standard deviation and number. Measurements by the author in the American Museum of Natural History, New York, USA and the Natural History Museum, Tring, U.K, and by Pamela C. Rasmussen of 6 *subsessor* in the Smithsonian Institution, Washington, D.C., USA. Includes 3 live males each of *microptera* and *marionae*. All measurements in mm.

	Wing	tail	tail/wing	bill length	bill depth	bill depth/ bill length	tarsus	tarsus/ wing	hind-claw
***assamica* male**	79.0-88.0	44.0-49.0	0.52-0.58	16.1-18.0	6.8-8.1	0.41-0.46	23.1-27.2	0.28-0.33	11.1-14.9
mean	83.7	46.5	0.55	17.0	7.5	0.44	25.0	0.30	13.0
S.D.	2.58	1.41	0.02	0.59	0.39	0.02	0.97	0.01	1.16
n	19	18	18	15	16	15	17	17	17
***assamica* female**	77.0-83.0	43.0-44.5	0.52-0.57	14.2-17.4	6.6-7.4	0.40-0.47	23.1-25.2	0.29-0.32	12.3-16.6
mean	79.8	43.6	0.55	16.2	7.1	0.44	24.3	0.31	13.6
S.D.	1.97	0.58	0.01	0.91	0.27	0.02	0.68	0.01	1.22
n	11	10	10	11	9	9	10	10	10
***affinis* male**	82.0-87.0	43.0-47.0	0.52-0.55	16.0-18.8	5.4-6.8	0.32-0.42	22.6-27.9	0.27-0.33	10.6-17.5
mean	85.0	45.3	0.53	16.8	6.1	0.36	25.6	0.30	12.6
S.D.	1.41	1.19	0.01	0.82	0.50	0.03	1.33	0.02	1.77
n	11	11	11	11	9	9	10	10	11
***affinis* female**	75.5-83.0	39.5-46.0	0.52-0.56	12.9-17.2	5.1-6.2	0.32-0.42	24.7-27.2	0.30-0.34	10.1-13.7
mean	79.4	42.2	0.53	15.4	5.6	0.36	26.0	0.33	11.8
S.D.	2.81	1.96	0.01	1.24	0.34	0.03	0.95	0.01	1.23
n	10	10	10	10	10	10	10	10	10
***microptera* male**	74.0-84.0	41.5-51.0	0.56-0.64	14.2-16.2	5.3-6.7	0.35-0.42	21.9-24.6	0.28-0.33	8.7-12.9
mean	77.6	46.2	060	15.2	5.9	0.39	23.4	0.30	10.2
S.D.	2.60	2.78	0.02	0.59	0.38	0.02	0.84	0.02	1.21
n	18	18	18	18	18	18	15	15	17
***microptera* female**	69.0-77.0	38.5-45.5	0.54-0.60	13.8-16.3	4.9-5.6	0.34-0.37	21.7-24.8	0.30-0.34	9.3-12.7
mean	73.1	41.9	0.57	14.7	5.3	0.36	23.4	0.32	10.6
S.D.	2.93	2.95	0.02	0.84	0.31	0.01	0.96	0.01	1.23
n	7	7	7	7	4	4	7	7	7
***marionae* male**	76.5-83.0	39.5-46.0	0.51-0.56	15.2-17.4	5.5-6.5	0.34-0.39	25.3-28.1	0.31-0.35	9.9-15.0
mean	80.5	42.2	0.53	16.4	6.0	0.36	26.7	0.33	12.2
S.D.	1.84	1.66	0.02	0.58	0.26	0.02	0.83	0.01	1.50
n	11	16	11	14	14	13	16	11	16
***marionae* female**	72.0-79.0	37.0-41.5	0.48-0.53	14.7-17.5	5.6-6.1	0.33-0.40	25.6-27.7	0.33-0.37	10.5-14.5
mean	76.4	38.7	0.51	15.6	5.8	0.37	26.5	0.35	12.9
S.D.	2.42	1.64	0.02	0.88	0.18	0.02	0.75	0.01	1.46
n	8	9	8	9	8	8	9	8	9
***subsessor* male**	78.0-82.0	38.5-41.0	0.49-0.51	15.2-16.7	5.7-6.1	0.34-0.40	25.8-28.4	0.32-0.35	11.4-13.3
mean	80.3	39.8	0.50	15.8	5.9	0.37	26.6	0.33	12.4
S.D.	2.08	1.77	0.01	0.65	0.21	0.03	1.24	0.01	0.90
n	3	2	2	4	3	3	4	3	4
***subsessor* female**	74.5-77.0	37.5-39.0	0.50-0.51	14.5-16.0	5.6-6.0	0.35-0.39	26.0-28.4	0.34-0.37	11.8-14.4
mean	76.2	38.2	0.50	15.4	5.8	0.37	27.4	0.36	13.4
S.D.	1.19	0.64	0.004	0.79	0.19	0.02	1.05	0.01	1.10
n	4	4	4	3	4	3	4	4	4

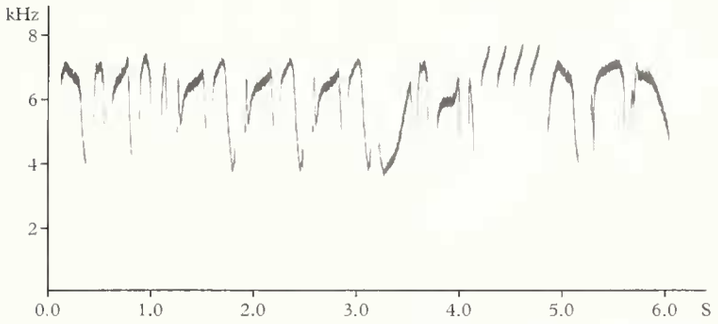

Figure 2. Sonagram terminology used in this paper. This figure shows one complete *strophe* consisting of 22 *elements* (separated from other strophes by a pause). Ten of the elements are arranged in *phrases*. One of these (a) consists of two different-looking elements, and this phrase is given three times, while another phrase (b) consists of four identical elements.

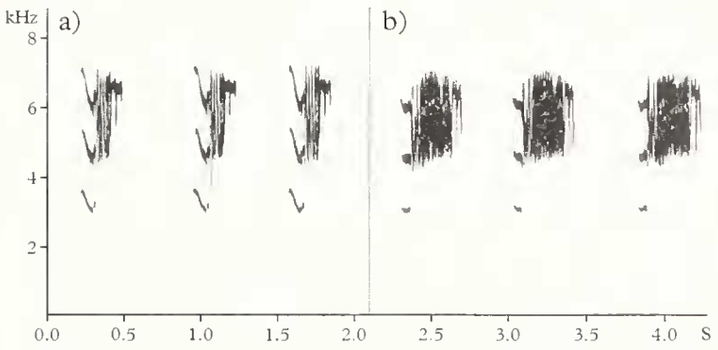

Figure 3. Part of common type of song of *assamica*, Chitwan, Nepal, March 1994. All tape recordings by Per Alström.

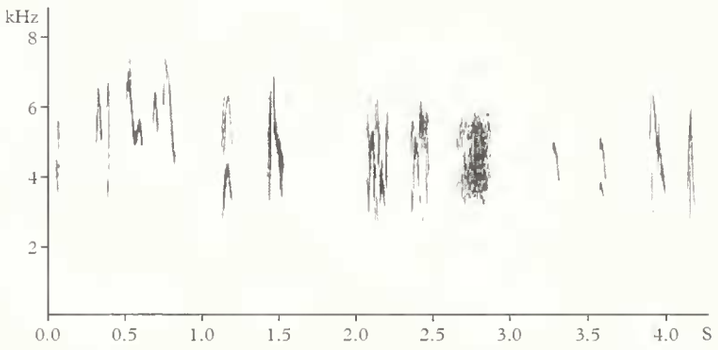

Figure 4. Part of less common type of song of *assamica*, Kaziranga, Assam, India, February 1994.

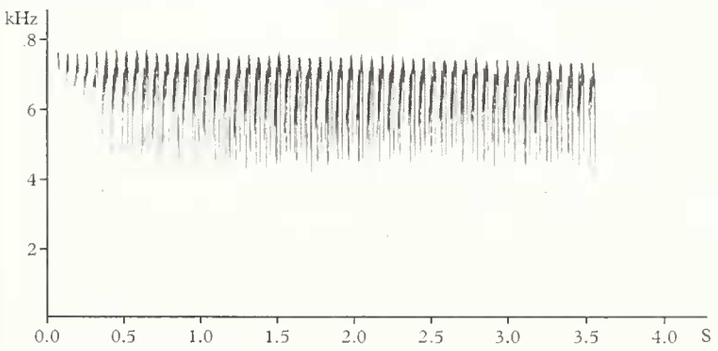

Figure 5. A complete song strophe of *affinis*, Hyderabad, Andhra Pradesh, India, February 1993.

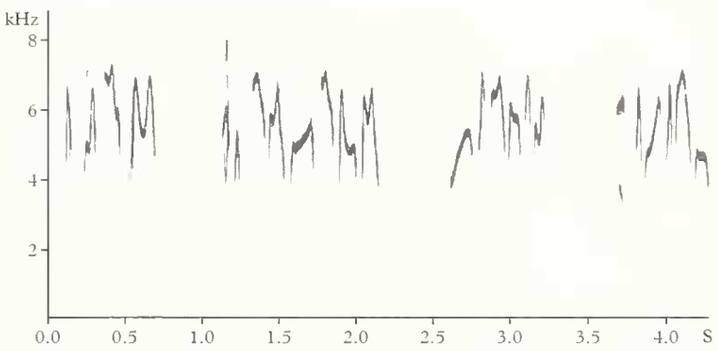

Figure 6. Part of type 1 song (4 strophes) of *microptera*, Bagan, Myanmar, March 1996.

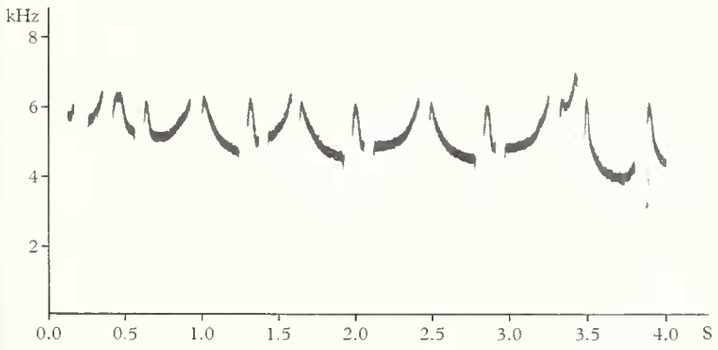

Figure 7. A complete strophe of type 2 song of *microptera*, Bagan, Myanmar, March 1996.

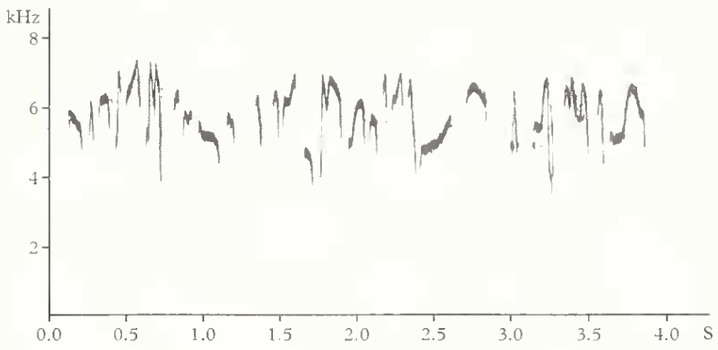

Figure 8. Part of type 3 song of *microptera*, Bagan, Myanmar, March 1996.

ground or a low perch, but occasionally also in flight. Ali and Ripley (1973) incorrectly state that the vocalizations of *assamica* are the same as those of *affinis*.

The song of *affinis* is a drawn-out (generally *c.* 3.5 s, up to *c.* 4.5 s) dry, metallic, rather high-pitched, 'straight' rattle, which could be transcribed as *zizizizezeze zezezezezezezezezezezezezezezezezeze* (Fig. 5). Sometimes a rapidly 'pumping' variant, which could be transcribed as *zerrr-zerrr-zerrr-zerrr-zerrr-zerrr-zerrr-zerrr-zerrr-zerrr*, is given. The song is delivered from a perch, often rather high (e.g. a tree, telephone wire etc.) and in a short song-flight (see Behaviour, below). The description of the song of *affinis* in Ali and Ripley (1973) appears to be a combination of the songs of *affinis* and *M. erythroptera* (these two are said to be 'almost identical', but this is not the case according to Alström *et al.* in prep.).

M. a. microptera has three different types of song:

Type 1: The commonest type consists of 3-10 short, high-pitched, squeaky, jingling, varied notes, delivered at a quick, almost explosive, pace (entire strophe on average slightly less than 1 s). Each strophe is generally given 2-4 times in succession, and the strophes are interspersed by rather long (usually a few seconds) pauses. In a 259 s long recording of one male 17 out of 62 strophes and 108 out

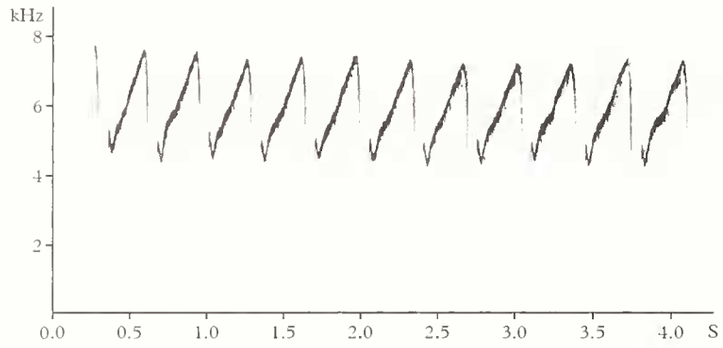

Figure 9. A complete song strophe of *marionae*, near Khao Yai, Thailand, April 1991.

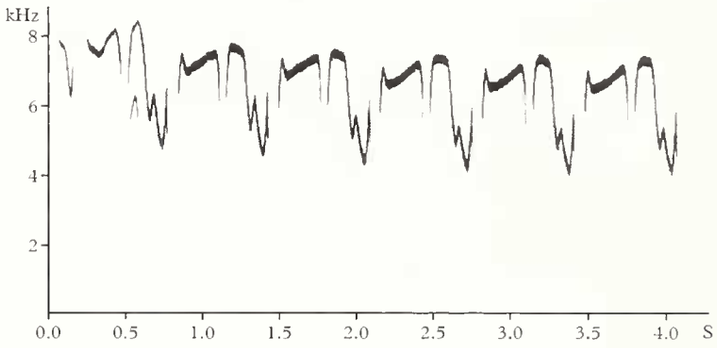

Figure 10. A complete song strophe of *marionae*, near Kaeng Krachan, Thailand, April 1996 (same individual as in Figs. 12 and 13).

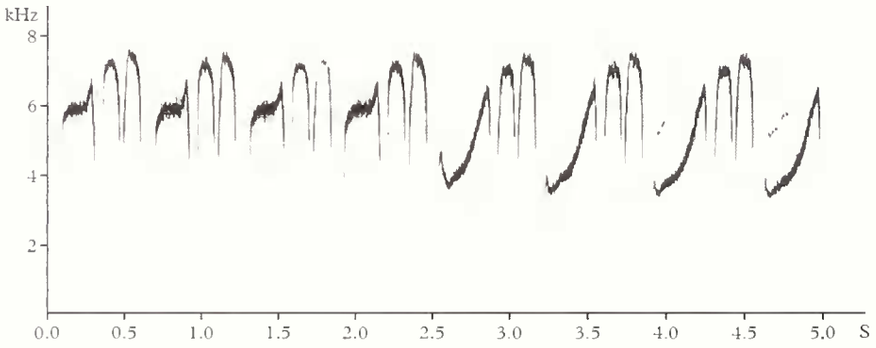

Figure 11. A complete song strophe of *marionae*, near Khao Yai, Thailand, March 1992.

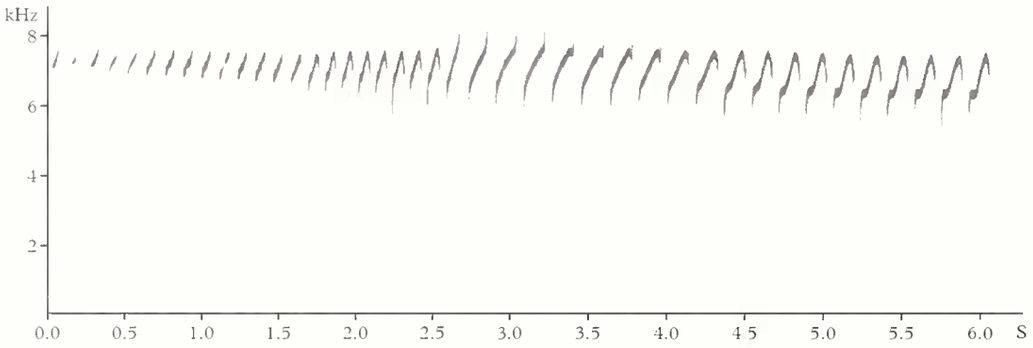

Figure 12. A complete song strophe of *marionae*, near Kaeng Krachan, Thailand, April 1996 (same individual as in Figs. 10 and 13).

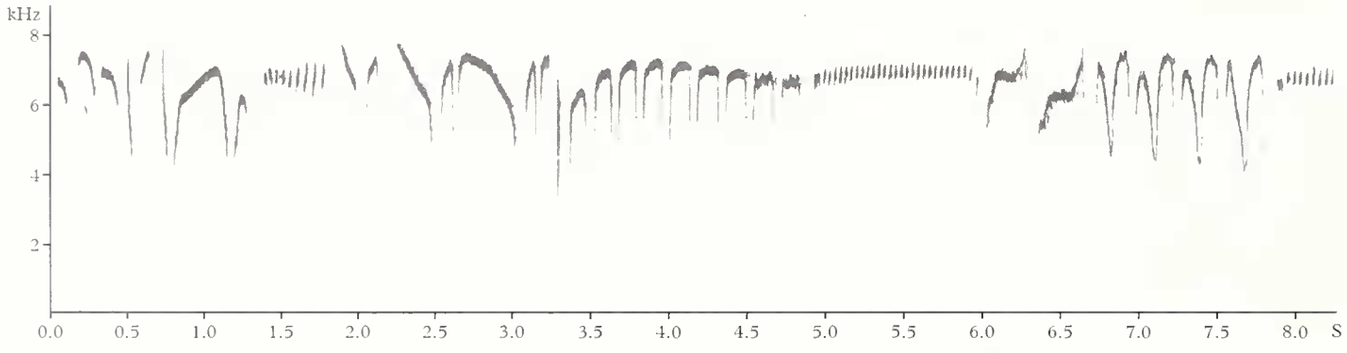

Figure 13. Part of atypical song of *marionae*, delivered in flight, near Kaeng Krachan, Thailand, April 1996 (same individual as in Figs. 11 and 12).

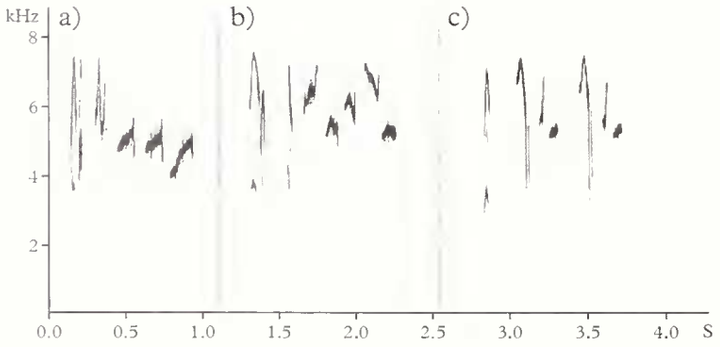

Figure 14. Calls of *assamica*, Chitwan, Nepal, March 1994.

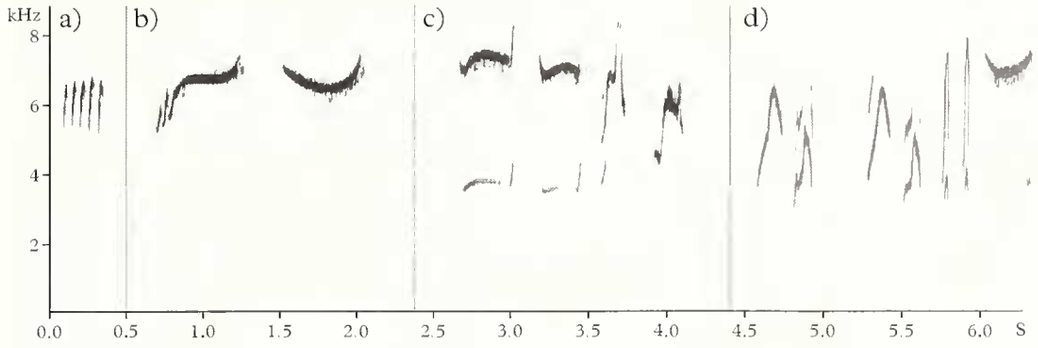

Figure 15. Calls of *affinis*, near Coimbatore, Tamil Nadu, India, February 1993.

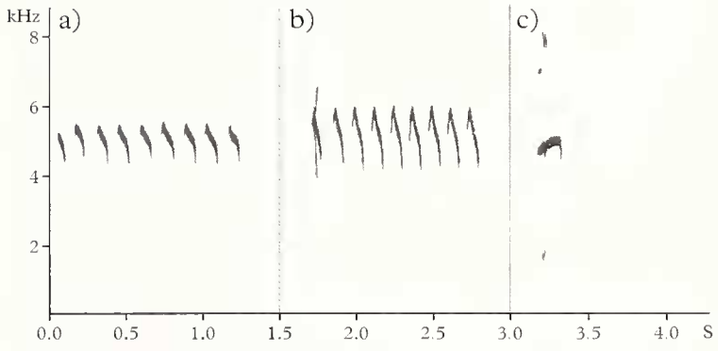

Figure 16. Calls of *microptera*, Bagan, Myanmar, March 1996.

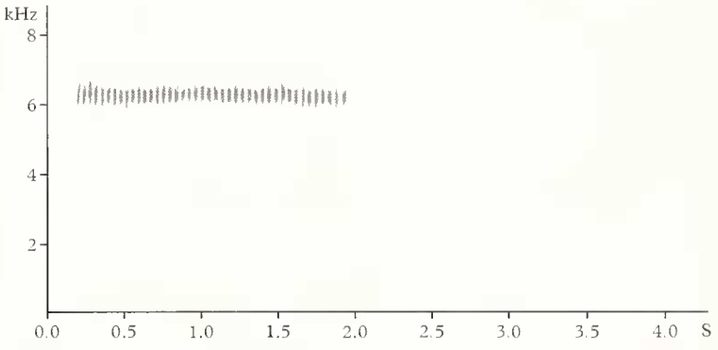

Figure 17. Call of *marionae*, near Khao Yai, Thailand, April 1991.

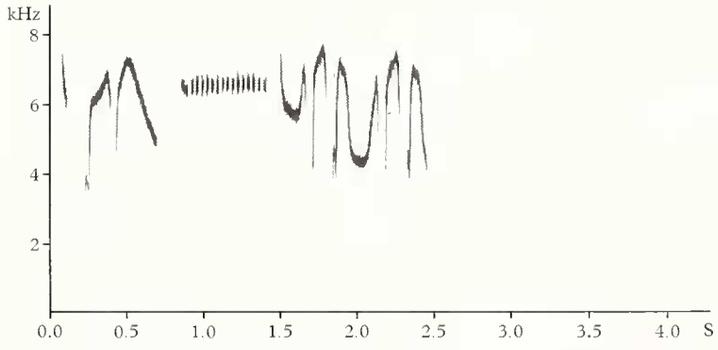

Figure 18. Call of *marionae*, near Khao Yai, Thailand, April 1991.

of 400 elements are unique. See Fig. 6 and Table 3. This song type is given from a perch, generally rather high up (e.g. a tree, a telephone wire or a building).

Type 2: This is markedly different from the first. Each strophe consists of 8-20 rather high-pitched notes, of which most (at least half) are markedly drawn-out (up to 0.37 s). The strophes average nearly 5 times as long as in the first type, and phrases occur in approximately 2/3 of the strophes (only rarely in the first song type). One example of a strophe could be transcribed as: *tsi(-)tsi(-)tsiü(-)tsüi(-)tsüü(-)tsi(-)ee(-)tsüü(-)tsi(-)eee(-)tsüü(-)tsi(-)eee(-)tsi(-)tsuu(-)tsiü* (Fig. 7). This song type is less common than the first. It is chiefly sung in a short, low song-flight (see Behaviour, below), apparently mainly when another male is suspected of intruding into the territory. It is also given from the ground or a low perch (e.g. a small rock, a mound of earth or a small bush). See Fig. 7 and Table 3.

Type 3: This has exclusively been noted in the high, prolonged song-flight (see Behaviour, below). It is basically similar to the first, although the strophes are on average more than twice as long (due to on average twice as many elements per strophe); the strophes are less often repeated; phrases are more common; and the pauses are on average distinctly shorter. Frequently, the song ends (during the descent) with the second song type. See Fig. 8 and Table 3.

All three types are different from the song of *affinis* and from the typical song of *assamica*. However, elements in the first and third types of song resemble some elements in both the 'jingling type' of song and in the calls of *assamica* (cf. Figs. 4, 14), and elements in all three types are reminiscent of elements in some of the 'calls' of *affinis* (cf. Fig. 15). For a comparison with *marionae*, see below.

The song of *marionae* is different from the songs of *assamica* and *affinis* (though more similar to 'calls' of the latter, see below). It is also different from *microptera*'s first and third types of song. It resembles *microptera*'s second type in several respects, although a careful comparison reveals differences (cf. Table 3). The song consists of high-pitched, thin, mostly drawn-out notes, which appear in phrases of 1-3 elements (Fig. 9-12); when the strophe is built up of only one repeated element, this element often gradually changes appearance (Fig. 12). The strophes are relatively long (*c.* 2-8 s, on average *c.* 4.5 s) and consist of up to *c.* 50 elements (on average *c.* 20). The strophes are interspersed by pauses of a

few seconds. Each strophe is often given 2-3 times in succession. A few examples of song-strophes could be transcribed as *tzi-tzeeep(-)tzeeep(-)tzeeep(-)tzeeep(-)tzeeep (-)tzeeep(-)tzeeep(-)tzeeep(-)tzeeep(-)tzeeep(-)tzeeep* (Fig. 9); *tzi(-)tzeee(-)tzeeut(-)tzeee(-)tzeeut(-)tzeee(-)tzeeut(-)tzeee (-)tzeeut(-)tzeee(-)tzeeut(-)tzeee(-)tzeeut* (Fig. 10); and *peeez(-)piz(-)piz-peeez(-)piz(-)piz-peeez(-)piz(-)piz-peeez(-)piz (-)piz-tzuueez(-)piz(-)piz-tzuueez(-)piz(-)piz-tzuueez (-)piz(-)piz-tzuueez.* (Fig. 11). The song is delivered from the ground or from a perch such as a fence post, telephone wire, small tree etc. The song is also now and then given in a short, low song-flight (see Behaviour, below).

On one occasion (in 1996), after a male *marionae* had been exposed to playback for considerable time, an extreme type of song was heard (Fig. 13). This was a continuous, drawn-out (16.9 s) ramble of various thin whistles ('cuts' from various strophes of the same individual's typical song, as well as other elements which may well have come from typical song, although I did not record these) and rattling calls (see below). Compared to typical song, there was a significantly higher proportion of different elements, as well as other differences (cf. Table 3). This song could be considered to consist of only one strophe, or of 5 strophes separated by calls (though there were no pauses). In several respects this song is actually more similar to the flight-song (type 3) of *microptera* than to typical song of *marionae* (cf. Table 3). The main differences from type 3 song of *microptera* are in the proportion of unique elements, the presence of phrases, and the presence of the diagnostic rattling calls (though note that one song of *microptera* which included an extremely high number of phrases had only a mean of 74.4% unique elements per strophe [n=13 unique strophes], and in the *microptera* song with the highest number of phrases 53.8% of 13 unique strophes had phrases). This song was delivered in a song-flight which was unusually long in duration, and during which the bird drifted sideways a longer distance than is usual in this taxon.

Calls

The calls of *assamica* are variable, thin, high-pitched, short notes, which are generally given in short, almost explosive series e.g. *tzrep-tzit(-)tzee(-)tzee(-)tzüü* (Fig. 14a), or *tzrep-tzit(-)tzee(-)tzüü(-)tzee(-)tzee(-)tzüü* (Fig. 14b). The calls of *assamica* are not closely similar to the calls of any other taxon (though somewhat reminiscent of the first and third types of song of *microptera*; see above).

M. a. affinis calls with a short (*c.* 0.25-0.3 s), high-pitched, thin, weak trill, *zir(-)ri(-)ri(-)ri(-)rit* (Fig. 15a). It also has various high-pitched, thin, generally drawn-out whistles and short, explosive, high-pitched notes. These are generally combined into short series, e.g. *drreeet eeet* (Fig. 15b); *ueeet-ueeet-dzip-dzüp* (Fig. 15c); or *dzeep-dzüp, dzeep-dzüp-tzi-tzi-eee* (Fig. 15d). Both of these types of calls have equivalents in *microptera* and especially *marionae* (see below). It should be noted that the second type has been considered to be song (Sivaprasad 1994). I cannot say for sure that these sounds do not have that function, although because they are uttered relatively infrequently, and because I have never heard them being given during the song-flight, I believe they are more likely to be calls.

M. a. microptera has three different types of calls: (1) short, high-pitched whistles, *heep* (Fig.16c); (2) quick series of high-pitched whistles, *tsi-tsi-tsi-tsi-tsi-tsi-tsi-tsi-tsi* (Fig. 16a-b); and (3) very faint, soft *tsüpp-tsüpp-tsüpp*, somewhat reminiscent of faint Long-billed Pipit *Anthus similis* calls. The third call has only been heard a few times by me, and only in flight. All of these calls are distinctive, although there are similarities between the first two and some of the calls of *affinis* and *marionae* (cf. Fig. 15 and 17, respectively).

M. a. marionae calls with a high-pitched, thin, metallic, drawn-out (*c.* 1.3-1.6 s), fast rattling trill, *tirrrrrrrrrrrrrrrrrrr* (Fig. 17), and, less commonly, with a hard, hammering series which could be transcribed as *tzet-tzet-tzet-tzet-tzet-tzet-tzet-tzet-tzet*. The first type is reminiscent of the trill given by *affinis*, but is significantly more drawn-out, faster and 'fuller' (cf. Fig. 15a). I have not heard *affinis* give an equivalent of the second type. It also has short series of thin, high-pitched, highly variable whistles which are reminiscent of, or identical to, song elements (Fig. 18), and which are often combined with the rattling trill. It is possible that these whistles are more appropriately classified as a variant type of song rather than as calls (cf. *affinis*, above), since at least some (all?) of the notes are identical to notes given in the typical song by the same individual. Moreover, the extreme type of song which was heard once (see above) was built up of a series of these whistling 'calls' (interspersed with trilling calls). However, the classification of these whistles as calls is suggested by the fact that they are given rather sporadically, and frequently in combination with trilling calls. These whistles are reminiscent of the equivalent whistles of *affinis*; all of the ones which have been analyzed differ between *marionae* and *affinis* (cf. Fig. 15b-d), but more research is needed on the individual variation in both taxa.

Behaviour

Song-flights

During the usual song-flight *assamica* rises to considerable height, where it flies about in random 'circles', alternating between a few quick wing-beats and short or slightly longer glides on spread and slightly raised wings and spread tail. This may go on for a few minutes before the bird drops to the ground. I have not noted any significant variation (out of at least 50-100 observed song-flights from the westernmost to the easternmost part of this taxon's range). When the variant type of song (see above) is given in flight, the wings are beaten continuously. The description of the song-flight given in Ali and Ripley (1973) (based on 'Baker') and in Sharma (1994) (presumably based on Ali and Ripley *op. cit.*), is confusingly different from my experience.

The song-flights of *affinis* and *marionae* are identical, while they are different from the song-flight of *assamica*. From the ground or, more commonly, from a perch on a mound of earth, a bush, fence post, small tree or telephone wire the bird ascends some metres and then parachutes down with its wings spread, slightly pushed forward and lifted in a shallow V, its tail spread, and its legs dangling (in agreement with Ali and Ripley 1973 [*affinis*] and Boonsong and Round 1991 [*marionae*]). The song-flight is generally performed rather infrequently, with long intervening periods during which the bird is singing while perched.

M. a. microptera has two different types of song-flight:

(1) One is performed in connection with the second type of song (see Vocalizations, above) and is almost identical to the song-flight of *affinis* and *marionae*. However, the bird usually takes off from the ground, and the song-flight is often repeated many times in succession, and each time the bird lands in a different spot (seemingly to scan the territory for an intruding male).

Table 3. Characteristics of songs of *microptera* and *marionae*. Note that the extreme song type of *marionae* has only been heard once (see text for further comments).

	***microptera* type 1 (perched)**	***microptera* type 2 (perched/ song-flight)**	***microptera* type 3 (song-flight)**		**marionae**	
			main part	end part (≈ type 2)	normal	extreme
number of elements per strophe	3-10 mean 6.1 S.D. 1.90 n=34 unique strophes	8-20 mean 16 S.D. 2.36 n=37 unique strophes	3-29 mean 12.3 S.D. 6.94 n=47 unique strophes	7-21 mean 14.4 S.D. 5.46 n= 5 unique strophes	*c.* 6-53 strophes mean *c.* 19.5 S.D. 7.97 n=49 unique strophes	*c.* 64, n=1 OR *c.* 6-15, mean *c.* 11.8, n=5 unique strophes
% different elements in a strophe	33.3-100 mean 95.2 S.D. 15.01 n=34 unique strophes	37.5-100 mean 73.1 S.D. 12.33 n=37 unique strophes	40-100 mean 91.4 S.D. 16.60 n=47 unique strophes	66.7-100 mean 87.1 S.D. 17.70 n=5 unique strophes	*c.* 3-41.2 strophes mean *c.* 15.6 S.D. 8.20 n=49 unique strophes	*c.* 61, n=1 OR *c.* 33-88, mean *c.* 67.8 n=5 unique strophes
length of elements	0.01-0.31 s mean 0.10 s S.D. 0.05 n=168 unique elements	0.02-0.37 s mean 0.18 s S.D. 0.10 n=81 unique elements	0.03-0.40 s mean 0.11 s S.D. 0.06 n=354 unique elements	0.05-0.45 s mean 0.21 s S.D. 0.10 n=52 unique elements	0.02-0.40 s mean 0.21 s S.D. 0.10 n=40 unique elements	0.02-0.34 mean 0.12 S.D. 0.08 n=39 unique elements
frequency range of elements (excluding harmonics if present)	0.5-3.7 kHz mean 2.05 kHz S.D. 0.73 n=74 unique elements	0.1-2.6 kHz mean 1.3 kHz S.D. 0.52 n=63 unique elements	0.5-4.5 kHz m. 1.75 kHz S.D 0.58 n=168 unique elements	0.4-2.3 kHz mean 1.23 kHz S.D. 0.45 n=51 unique elements	0.8-3.7 kHz mean 2.50 kHz S.D. 0.08 n=31 unique elements	0.4-4 kHz mean 1.99 S.D. 0.87 n=38 unique elements
other characteristics of elements	generally rather 'sharply bent' (i.e. marked frequency variation in same element)	Usually rather smoothly curved; generally centred around *c.* 6 kHz (between 5 and 7 kHz)	as *microptera* type 1	as *microptera* type 2	generally rather "sharply bent"; on average higher-pitched than *microptera* type 2	as *marionae* typical song
presence of phrases in a strophe	5.9% n=34 unique strophes	66.7% n=18 unique strophes	23.9% n=46 unique strophes	60% n=5 unique strophes	100% n=65 unique strophes	(100%, n=1) OR 80%, n=5 unique strophes
length of strophes	0.4-1.4 s mean 0.88 s S.D. 0.27 n=33 unique strophes	2.7-5.6 s mean 4.18 s S.D. 0.78 n=10 unique strophes	0.5-5.5 s mean 2.00 s S.D. 1.32 n=47 unique strophes	1.8-5.4 mean 3.68 S.D 1.48 n=5 unique strophes	2-8 s mean 4.50 s S.D. 1.16 n=65 unique strophes	16.9 s, n=1 OR 1.2-3.1 s, mean 2.30 s, n=5 unique strophes
number of times a particular strophe is sung	1-8 mean 3.54 S.D. 3.67 n=78 unique strophes	1-6 mean 2.38 S.D. 3.73 n=19 unique strophes	1-4 mean 1.40 S.D. 3.59 n=74 unique strophes	1-2 n= 5 unique strophes	1-7 mean 1.91 S.D. 3.55 n=44 unique strophes	(1, n=1) OR 1, n=5 unique strophes
length of pauses between strophes	1.4-7.4 s mean 3.3 s S.D. 1.11 n=91 pauses	1.5-5.2 s mean 2.81 s S.D. 0.88 n=29 pauses	0.2-2.5 s mean 1.1 s S.D. 0.64 n=69 pauses	0.5-1.4 s mean 0.93 s S.D. 0.45 n=3 pauses	1.6-6.5 s mean 3.6 s S.D. 1.07 n=42 pauses	(none, n=1) OR 0.48-1.72 s, mean 0.98, n=4

(2) The other is performed in connection with the third type of song (see Vocalizations, above). From a perch, often rather high, the bird ascends quickly (while singing) to considerable height, where it circles erratically for up to more than a minute. During the circling phase, the bird flies with quick, slightly jerky wing-beats and spread tail; rarely the wings are momentarily held out stiffly. The descent is a silent plunge. Alternatively, the bird parachutes down just like in the first type of song-flight (while singing the second type of song [see Vocalizations, above]; the last part of the descent is a silent plunge, though). This song-flight is most similar to the song-flight of *assamica*, but it lacks this taxon's regular glides on spread wings during the circling phase (which is the case also in *assamica* when its variant type of song is delivered). Moreover, *microptera*'s parachuting descent has not been seen in *assamica*, and *microptera*'s song-flight is of shorter duration on average.

Smythies (1986) describes the first of *microptera*'s two types of song-flights, while the second is only mentioned in passing ('though it occasionally soars quite high'). In my experience of at least 50-100 song-flights, both types are roughly equally common.

I have occasionally heard *microptera* clap its wings while ascending, a behaviour known in some African *Mirafra* larks, e.g. Clapper Lark *M. apiata* (Keith *et al.* 1992, Sinclair *et al.* 1993), and which has also been observed in *Mirafra erythroptera* (Alström *et al.* in prep.).

Other

The taxon *assamica* is almost entirely terrestrial, rarely perching above the ground. In contrast, *affinis*, *microptera* and *marionae* frequently perch in bushes, trees, on telegraph wires etc. Especially *affinis* and *microptera* frequently land in trees when flushed off the ground, and I have seen both sitting in trees at least 10 m above the ground.

M. a. microptera frequently raises its crown feathers. I have not noted this behaviour in the other taxa.

Habitat

The taxa *affinis*, *microptera* and *marionae* inhabit dry, open areas with bushes and trees, and even occur in scrubby glades in well-wooded areas. *M. a. assamica*, on the other hand, favours less shrubby and less wooded, more grassy, and often slightly wet habitats.

Distributions

All of the taxa are largely allopatric, but there are some suggestions that two forms overlap in some areas.

Macdonald (1906) stated that *assamica* occurred in sympatry with *microptera* in the Myingyan district of Myanmar. This could not be confirmed because I did not find *assamica* or *marionae* anywhere in Myanmar, despite visiting several localities with suitable habitat.

Ball (1874, 1878) reported that the ranges of *assamica* and *affinis* overlap locally in southeast Bihar, India. In addition, Abdulali (1976) mentioned specimens of *affinis* from south of this area in northern Orissa. These were darker and greyer above than typical *affinis*, though 'quite different from the dark grey of nominate *assamica*, but resemble them in their noticeably heavy bills, and represent an intermediate population between *affinis* and *assamica*, closer to the former'. Unfortunately I have not examined any specimens from that area.

DISCUSSION

The morphological differences between *assamica*, *affinis*, *microptera* and *marionae* are slight, yet they are so pronounced that I have not seen any specimens (neither in the field nor in museum collections) which have been unidentifiable. In some respects *marionae* and especially *affinis* and *microptera* are more similar to *Mirafra erythroptera* than either is to *assamica* (Alström *et al.* in prep.). *M. erythroptera* is sympatric with *assamica* (Vaurie 1951, Ali and Ripley 1973; pers. obs.) and *affinis* (Whistler 1935, Whistler 1949, Vaurie 1951, Ali and Ripley 1973, pers. obs.). The differences in vocalizations between *assamica*, *affinis*, *microptera* and *marionae* are pronounced and consistent. The differences are at least as well marked as the differences between any of them and *Mirafra erythroptera* (Alström *et al.* in prep.), and especially the songs actually differ more between *assamica*, *affinis*, *microptera* and *marionae* than between congeneric species of other Eurasian larks (cf. Cramp 1988, Alström *et al.* in prep.). The differences in song-flight between *assamica*, *microptera* and *affinis/marionae* are distinct. In contrast, the song-flights of congeneric species of other Eurasian larks differ little or not at all (cf. Cramp 1988, Alström *et al.* in prep.). The differences in other behavioural aspects between *assamica* and the others are also remarkable in comparison with other closely related Eurasian larks, while the differences in habitat choice are on a par with those of congeneric species of larks (cf. Cramp 1988, Alström *et al.* in prep.).

If the phylogenetic species concept *sensu* Cracraft (1983, 1989) is applied, all four taxa are separate species, since they are all diagnosably different and represent separate lineages. The biological species concept (*sensu* Mayr 1942, 1986) is problematical to apply, since all of the taxa may be allopatric. The songs of male passerines are generally considered to be important in female attraction (review in Catchpole and Slater 1995). It seems reasonable to assume that in sexually monomorphic, cryptically coloured species such as larks, songs and distinctive sexual displays (such as song-flights) are particularly important in female attraction. Because in most cases it would be selectively disadvantageous for a female to mate with a male of a different species (though see Grant and Grant 1992, who reported higher fitness in hybrids between two species of *Geospiza*-finches than in their respective parental species), selection can be assumed to favour discrimination between their own species's song and song of different species. Accordingly, at least in species lacking prominent visual signals, song presumably acts as a prezygotic reproductive isolating mechanism between different sympatric species (though Baptista and Trail 1992 remarked that evidence for this hypothesis is lacking). It seems likely that the highly distinctive songs of *assamica*, *microptera*, *affinis* and *marionae* and different song-flights of *assamica*, *microptera* and *affinis/marionae* would prevent interbreeding if their ranges would meet. The different habitat choice of *assamica* compared to the others would further minimize the chances of interbreeding between *assamica* and the others.

To conclude, irrespective of which species concept is applied, I consider *assamica*, *affinis*, *microptera* and *marionae* to be best considered separate species. Several English names have been used in the past. I suggest the following names be used: Bengal Bushlark for *M. assamica* (*sensu stricto*), Jerdon's Bushlark for *M. affinis* (after the person

who first described it), Burmese Bushlark for *M. microptera* and Indochinese Bushlark for *M. marionae*.

A molecular study is being undertaken, so it is hoped that a phylogenetic hypothesis will be formulated in the future.

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